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Title: HERITABILITY ESTIMATES AND ASSOCIATIONS
OF DIFFERENT HEIGHT LEVELS WITH ALUMINUM
TOXICITY AND GRAIN YIELD IN WHEAT

Abstract approved: Redacted for privacy
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Standard height, low grain yield potential, Al tolerant cultivars BH 1146 and Atlas 66, and semidwarf, high grain yield potential cultivars Tordo and Siete Cerros which differ in their sensitivity to Al were crossed in a diallel manner. Parents, F_1 's, F_2 's and reciprocal backcrosses were tested for their seedling reaction using a nutrient solution technique. Subsequently, plants representing all crosses and generations tested were transplanted to the field where plant height and grain yield were determined on an individual plant basis.

Seedlings were screened using different concentrations of soluble Al to determine the nature of inheritance of the four cultivars to Al toxicity. It was observed that at 2 ppm of Al, Tordo was tolerant differing from Siete Cerros by one dominant gene. At 3 ppm, both Tordo and Siete Cerros were sensitive while BH 1146 and Atlas 66 had one and two genes respectively for tolerance. BH 1146 and Atlas 66

had a different gene conditioning tolerance to 6 ppm while BH 1146 continued to show one dominant gene for tolerance even at 10 ppm. Atlas was sensitive at this latter concentration. It is concluded that BH 1146 would be the most promising source of tolerance to higher levels of Al present in acid soils.

Heritability estimates and associations among traits for populations studied were first evaluated at 6 ppm of Al. Narrow sense heritability and coefficient of determination estimates for reaction to Al toxicity, plant height and grain yield were obtained from regression of F_2 means on F_1 means and from F_1 mean and F_2 mean correlations, respectively.

Correlations were determined on an individual plant basis for parents, F_1 's and F_2 's. Genotypic correlations were computed based on phenotypic correlations (F_2), environmental correlations (F_1) and narrow sense heritability estimates.

Heritability estimates for plant height and Al tolerance were high with the value being intermediate for grain yield. Genotypic, phenotypic and environmental correlations between Al tolerance with plant height and grain yield respectively were not significant. Grain yield and plant height correlations were positive and highly significant.

Results suggest it would be possible to select plant types with semidwarf height levels with Al tolerance and high potential grain yield, however, large F_2 populations will be required. Tordo would

be the most promising in developing semidwarf cultivars adapted to soil where Al is a limiting factor. However, Siete Cerros would be preferred due to the poor seed quality associated with the Tom Thumb dwarfing gene in Tordo.

Heritability Estimates and Associations of Different
Height Levels with Aluminum Toxicity and
Grain Yield in Wheat

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Typed by

Opal Grossnicklaus for Carlos Eduardo de Oliveira Camargo

WITH LOVE TO:

Maria Catarina, my wife

Carlos and Daniel, my sons

Francisca, my daughter

Leocadio and Celia, my parents

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Heritability Estimates and Associations of Different Height Levels
with Aluminum Toxicity and Grain Yield in Wheat.¹

C.E.O. Camargo, W. E. Kronstad and R. J. Metzger²

ABSTRACT

Standard height, low grain yield potential, Al tolerant cultivars BH 1146 and Atlas 66, and semidwarf, high grain yield potential, Al sensitive cultivars Tordo and Siete Cerros were crossed in a diallel manner. Parents, F_1 's, F_2 's and reciprocal backcrosses were tested for their seedling reaction to 6 ppm of Al at 25°C using a nutrient solution technique. All plants were subsequently transplanted to the field where plant height and grain yield were determined on an individual basis.

Additional index words: Triticum aestivum L em Thell, Dwarf, Semidwarf, Root regrowth, Aluminum tolerance, Aluminum sensitivity, Acid soil, Coefficient of Correlation, Coefficient of Determination, Narrow sense heritabilities.

¹Contribution of the Crop Science Dep., Oregon Agric. Exp. Stn., Corvallis. Part of a thesis submitted by the senior author in partial fulfillment of the requirements for the Ph.D. degree at Oregon State Univ.

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Narrow sense heritability and coefficient of determination estimates for reaction to Al toxicity, plant height and grain yield were obtained from regression of F_2 means on F_1 means and from F_1 mean and F_2 mean correlations, respectively. Correlations for crosses were determined on an individual plant basis for parents, F_1 's and F_2 's. Genotypic correlations were computed based on phenotypic correlations (F_2), environmental correlations (F_1) and narrow sense heritability estimates.

Heritability estimates for plant height and Al tolerance were high with the value being intermediate for grain yield. Genotypic, phenotypic and environmental correlations between Al tolerance with plant height and grain yield, respectively, were not significant. Grain yield and plant height correlations were positive and highly significant.

Results suggest it would be possible to select plant types with semidwarf height levels with Al tolerance and high potential grain yield; however, large F_2 populations will be required. Tordo would be the most promising in developing semidwarf cultivars adapted to soil where Al is a limiting factor. However, Siete Cerros would be preferred due to the occurrence of poor seed quality associated with the Tom Thumb dwarfing gene in Tordo.

INTRODUCTION

Aluminum toxicity has been identified as a major limiting factor to wheat production on acid soils (Silva, 1976). Cultivars developed under such conditions are tall, susceptible to lodging and have a small number of fertile florets and kernels per head resulting in low grain yield potential.

Semidwarf cultivars have significantly increased the grain yield potential mainly through greater lodging resistance and sink size (Pepe et al., 1975) but they are not adapted to acid soil conditions where high levels of soluble Al are present.

Differences in Al tolerance among cultivars of the same plant species suggest the possibility of increasing the Al tolerance of commercial cultivars through plant breeding (Foy et al., 1965). Kerridge and Kronstad (1968) found a single dominant gene for Al tolerance at 1.6 ppm in a cross between a moderately tolerant and a sensitive wheat cultivar. Since the moderately tolerant parent was less tolerant than other known cultivars they postulated that one or more major genes with several modifying genes may be available in other sources of germ plasm.

It is very difficult to adequately control a soil system so that the degree of Al "insult" can be reproduced from experiment to experiment or from location to location. Further Al toxicity is not the only limiting factor in acid soils, thus screening methods using acid soils are usually not precise enough. The plant part most

directly affected, the root system, is also not easily observed. Nutrient solution techniques provide an efficient nondestructive screening method for use in the development of Al tolerant wheat cultivars (Moore et al., 1976 and Lafever et al., 1977).

A rapid reproducible screening technique was developed (Kerridge, 1969, Ali, 1973 and Moore et al., 1976) based on irreversible damage to the primary root meristem in the seedling stage. Four classes of tolerance were identified on the basis of the appearance of the root tips following a "pulse insult" of Al.

It was the objective of this study to determine the nature of the associations between plant height, Al toxicity and grain yield in selected wheat crosses. A second goal was to identify the most promising source of dwarfism to obtain short stature combined with tolerance to Al toxicity and greater yield potential.

MATERIALS AND METHODS

The four cultivars, which were crossed in a diallel manner, represented a range of height levels and reaction patterns to soluble Al concentrations. Standard height cultivars BH 1146 and Atlas 66 were developed under acid soil conditions and have been reported to be tolerant to high levels of soluble Al. They are also quite low with regard to their grain yield potential. The two semidwarf cultivars Siete Cerros and Tordo represent the Norin 10/Brevor 14 and the Tom Thumb sources of dwarfism, respectively. Both cultivars are sensitive to low levels of soluble Al, but do represent potential sources of high grain yield.

The screening technique for Al toxicity used has been described by Moore et al. (1976). Modifications made in this study were that the Al treatment solution used contained one-tenth of the total nutrients present in the basal (recovery) solution, with phosphorus omitted and iron maintained at full strength. These procedures reduced the Al concentration necessary to characterize the classes of tolerance and to eliminate the possibility of Al precipitation (Ali, 1973).

Parents, F_1 's, F_2 's and backcrosses to the tall parent (BC_1) and to the semidwarf parents (BC_2) were screened for tolerance in nutrient solution containing 6 ppm of Al. This concentration was selected based on preliminary studies conducted to establish a level where tolerant and sensitive types could be easily identified. In each of five replications 30 seedlings were screened for each parent, F_1 ,

BC₁, and BC₂. Sixty seedlings of each F₂ population were tested. The cultivars 'Brevor' and 'Chinese Spring' (susceptible to 6 ppm of Al) were used as controls in all replications. After determining the amount of root regrowth following exposure to Al, the seedlings were removed from nutrient solution and planted in peat moss pots containing fertilized and limed soil. After one week in the greenhouse the plants were hardened outside for three weeks prior to transplanting to the field.

A randomized block design composed of 28 entries which included four parents, six F₁'s, F₂'s, BC₁'s and BC₂'s, respectively, was used. Three row plots were used for parent, F₁'s, BC₁'s and six row plots were used for F₂'s. Each replication consisted of 102 rows, each row 3 m long with 30 cm spacing between rows. Ten seedlings were spaced 30 cm apart within each row. Five replications were utilized.

Data were collected on an individual plant basis, as follows:

Aluminum tolerance was measured as the length (mm) of root regrowth of the central primary root of each seedling after 72 hours in complete recovery nutrient solution.

Plant height was measured in cm from the soil surface to the tip of the spike of the tallest culm.

Weight of grain harvested from each plant represented grain yield.

All the characters under study were subjected to analysis of variance with the F test used to determine significant differences. Plot per generation means were used for the analysis. The generation

effects in the analysis of variance were divided into component effects to detect differences between and within generations.

Narrow sense heritability estimates were obtained from the regression of F_2 means on F_1 mean values as described by Falconer (1960). Coefficients of determination were also obtained from F_1 mean- F_2 mean correlations across all crosses. Phenotypic, environmental and genotypic correlations were used to estimate the degree of association between each pair of agronomic traits. As suggested by Falconer (1960), the F_1 and F_2 correlations were considered as environmental and phenotypic correlations, respectively. The genetic correlations were calculated from the formula

$$r_{ph} = \sqrt{H_x} \sqrt{H_y} r_G + \sqrt{E_x} \sqrt{E_y} r_E$$

where r_{ph} = phenotypic correlations between x and y, r_G = genotypic correlation between x and y, r_E = environmental correlation between x and y, H = heritability, with subscript x or y according to the trait, $E = 1 - H$, also with subscripts according to the trait.

RESULTS AND DISCUSSION

Parental cultivars used represented a range in genetic diversity for plant height, tolerance to Al toxicity and grain yield. To test the significance of these genetic differences, an analysis of variance was computed among genotypes, and among and within generations for all three characters measured. Significant differences ($p=.01$) were observed among genotypes, and among and within generations for all characters studied. The within generations results from the analysis of variance confirm the assumption that genetic diversity existed among parental lines.

Heritability estimates for tolerance to 6 ppm of Al and plant height were high and intermediate for grain yield (Table 1). This indicates that a large part of the total genetic variability associated with the three measured traits was the result of additive gene action or genes which behave in an additive manner. The coefficients of determination are also listed in Table 1. High r^2 values were also obtained for tolerance to Al and plant height and a low r^2 value was obtained for yield of grain. Thus selection in the F_2 or F_3 generations for either plant height or tolerance to Al toxicity would be effective. The intermediate heritability estimate and low r^2 value indicate that selection for grain yield should be delayed until later generations when more precise estimates of the genetic worth of the progeny could be determined.

Table 1. Narrow-sense heritability estimates and coefficient of determination values for root regrowth at 6 ppm of aluminum, plant height and grain yield for F_1 's and F_2 's in a four parent diallel cross in wheat.

Character	Narrow-sense heritability, \underline{h}	Coefficients of determination r^2
Tolerance to aluminum	.944 \pm .182	.520**
Plant height	.903 \pm .043	.959**
Yield/plant	.507 \pm .126	.271**

**Significant at 1% probability level.

Simple correlation coefficients for parents, F_1 's and F_2 's separately and for all genotypes together including backcrosses to respective parents were calculated to evaluate the possible associations between traits within each cross (Table 2). The environmental (F_1), phenotypic (F_2) and genotypic correlation coefficients between tolerance to Al and plant height for all crosses were low and not significant. The correlation between the same traits for parents only and all genotypes together were positive and highly significant (.01). There was one exception, the cross BH 1146/Atlas 66, where the correlation value was negative and significant. This can be explained since BH 1146 is more tolerant to 6 ppm of Al whereas Atlas 66 is less tolerant and taller.

Table 2. Association of root regrowth at 6 ppm of aluminum with plant height and yield for parents, F_1 's and F_2 's in wheat.

Characters correlated within crosses	Parents only	F_1 only (r_E) ⁽¹⁾	F_2 only (r_{Ph}) ⁽²⁾	r_G ⁽³⁾
<hr/>				
Tolerance to Al + vs. height				
BH 1146/Tordo	.843**	-.143	.001	.013
BH 1146/Siete Cerros	.751**	-.033	.031	.036
Atlas 66/Tordo	.896**	-.084	-.003	.010
Atlas 66/Siete Cerros	.895**	-.095	-.080	-.079
BH 1146/Atlas 66	-.249**	-.005	.029	.032
Tordo/Siete Cerros	--	--	--	--
<hr/>				
Tolerance to Al + vs. yield				
BH 1146/Tordo	.619**	-.056	.085	.136
BH 1146/Siete Cerros	.022	-.004	-.027	-.046
Atlas 66/Tordo	.726**	-.036	-.006	.000
Atlas 66/Siete Cerros	.471**	.066	-.006	-.025
BH 1146/Atlas 66	-.165**	.057	.042	.047
Tordo/Siete Cerros	--	--	--	--
<hr/>				
Height vs. yield				
BH 1146/Tordo	.775**	.527**	.281**	.245
BH 1146/Siete Cerros	.274**	.369**	.351**	.399
Atlas 66/Tordo	.827**	.456**	.377**	.411
Atlas 66/Siete Cerros	.543**	.530**	.466**	.517
BH 1146/Atlas 66	.531**	.465**	.168**	.098
Tordo/Siete Cerros	.813**	.608**	.497**	.539
<hr/>				
Minimum pop size	262-289	135-143	281-296	

(1) environmental correlation

(2) phenotypic correlation

(3) genetic correlation

** significant at 1% level of probability

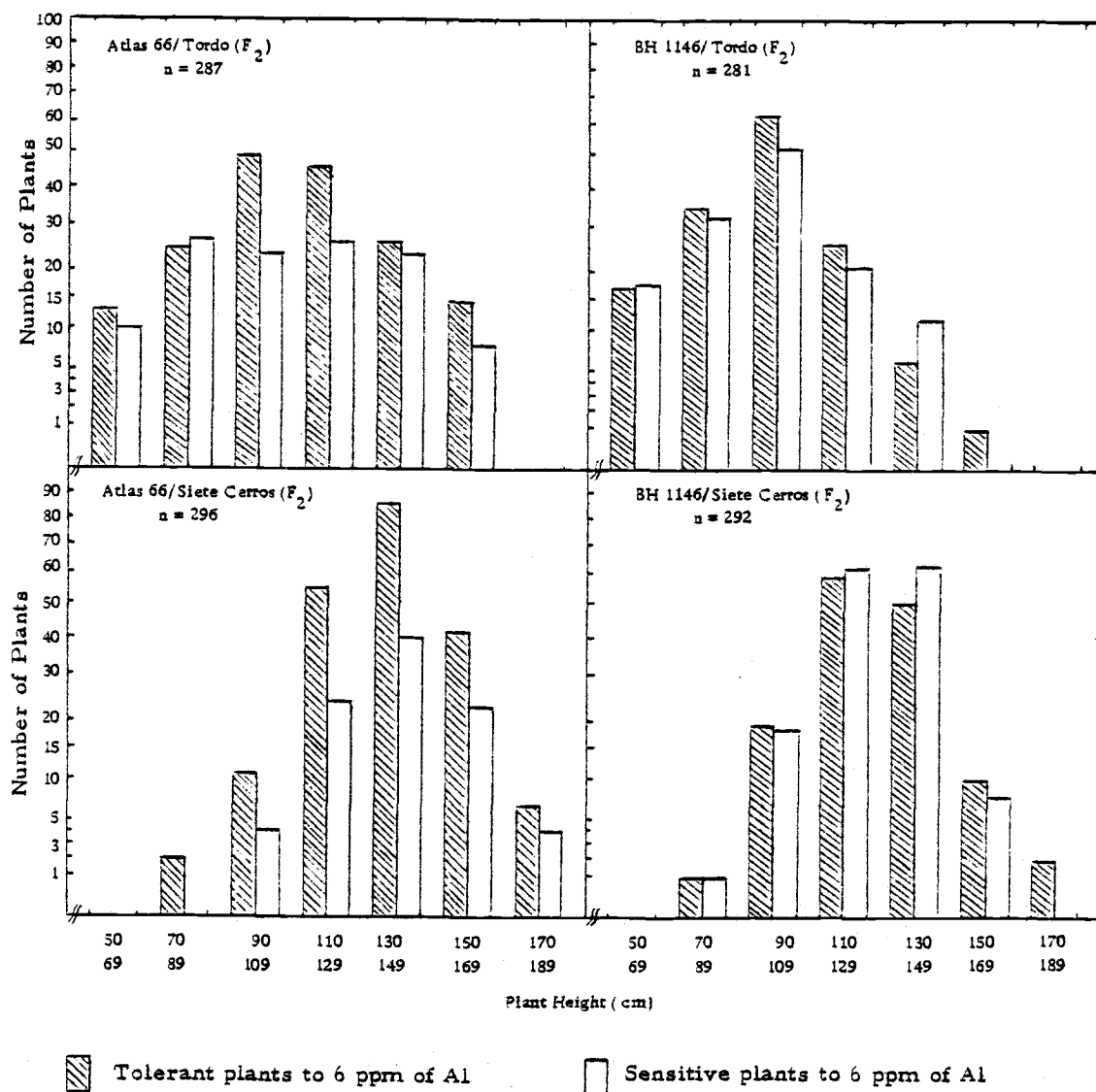
The genetic correlation values for the relationship between tolerance to Al and plant height suggest that it is possible to select within the segregating populations for semidwarf plants with tolerance to Al.

The environmental, phenotypic and genotypic correlation between tolerance to Al and yield of grain were all small and nonsignificant. This suggests that it would be possible to select for tolerance to Al toxicity in early generations and for yield, within the previously selected tolerant populations in later generations.

Height and yield correlations were also computed for all crosses (Table 2). The correlation coefficients for parents, F_1 's and F_2 's separately and for all genotypes together were positive and highly significant ($p=.01$). In general the magnitude of the phenotypic correlation (F_2) and genetic correlation was consistent for all crosses. Despite a positive association between grain yield and plant height, it would be possible to select Al tolerant semidwarf types from populations segregating for plant height involving the parents studied.

Segregating populations from crosses between the tall cultivars and the two different sources of dwarfism (Figure 1) indicate that both short stature sources could be used efficiently in a breeding program toward the development of semidwarf and Al tolerant wheat cultivars. However, large F_2 populations would be required to ensure the frequency of desired recombinants. Tordo would be the best source due to the higher frequency of short statured individuals with Al tolerance. The same source of dwarfism would be more promising

Figure 1. Number of tolerant and sensitive plants to 6 ppm of aluminum associated with plant height in four crosses involving tolerant/sensitive wheat cultivars.



when combining tolerant semidwarf cultivars with grain yield. However, Siete Cerros would be preferred due to the occurrence of poor seed quality associated with the Tom Thumb dwarfing gene in Tordo.

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